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CRONARTIUM COMPTONIAE, THE SWEETFERN BLISTER RUST OF PITCH PINES

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INTRODUCTION

The obvious destructive effect of the stem-inhabiting *Peridermiums* upon their pine hosts has attracted attention from the first. These fungi are also of unusual scientific interest because of their involved life history, in which they pass through two distinct phases on entirely unrelated hosts. In many cases the pines attacked are of minor commercial importance, but some of the most valuable species are liable to especially severe attacks when brought by man into contact with these fungi. During the last 25 years the knowledge of *Peridermiums* and their destructive possibilities has greatly increased. The sweetfern blister rust, *Cronartium comptoniae* Arthur, is possibly the most common and widely distributed species occurring on pitch pines in eastern North America. This species has proved particularly dangerous to forest-tree nurseries producing pitch-pine stock. With the rapid and unprecedented increase in output of such nurseries, danger from this and related fungi is certain to increase. A great deal of the work of these nurseries will have to be repeated unless the young trees they are producing are carefully guarded. Little reliance can be placed on species from other regions until something is known of their reaction to these fungi.

¹ The writers are indebted to the authorities of the following institutions for information and free access to their collections: British Museum of Natural History; Kew Gardens; Herbarium of the Dominion Botanist, Ottawa, Canada; Farlow Herbarium; Boston Society of Natural History; Essex Institute at Salem, Mass.; Brooklyn Botanic Garden; New York Botanical Garden; New York State Museum; New Hampshire Agricultural Experiment Station; Dartmouth College; Middlebury College; University of Vermont; New York State College of Forestry at Syracuse; Minnesota Agricultural College. Also the private herbaria of J. C. Arthur, J. J. Davis, J. R. Weir, and John Dearness.

HISTORY OF THE DISEASE

Before 1910 the sweetfern blister rust was known to occur occasionally on a number of species of the pitch pines. Its occurrence was mostly a matter of curiosity rather than of apprehension. At about this time it was reported to have attacked pitch-pine seedlings in some of the nurseries that produced forest planting stock, and even to have caused damage in plantations made with stock from infected nurseries. The most striking instance of such damage was in plantations of western yellow pine, *Pinus ponderosa* Douglas,² and lodgepole pine, *P. contorta* Loudon, at Roscommon, Mich. (18, 33, 44, 45).³ The seedlings were grown in a nursery at that place. The sweetfern, *Comptonia asplenifolia* L., the most common alternate host of this fungus, was very abundant for miles around the nursery, and the fungus was present in that region on the native jack pine, *P. banksiana* Lambert, so that abundant spores of the fungus were produced and blown by the wind everywhere in the vicinity. Very heavy infection resulted, and in spite of attempts to sort out the infected trees the plantations were practically a total loss.

Numerous cases have come to the writers' attention where forest-tree nurseries have sustained considerable damage from the attacks of this disease. In every case of this kind it has been found that the nurseryman is in no way to blame for bringing the disease into the locality, but that it was already native there and spread into the nursery from outside as it did in the above-mentioned instance. It has, however, been carried into new localities on infected nursery stock, notably to St. Louis, Mo., and Cincinnati and Wooster, Ohio. Other cases are also known. This phase of its distribution is one that needs careful attention by nurserymen when shipping stock of the pitch pines for any distance.

SYMPTOMS

Because of the rough bark of the pitch pines, even at a relatively young stage of growth, this disease is not easy to detect except when the blisters are present or in cases of several years' standing. There is a tendency toward the formation of a slight swelling of the affected twig or stem. Small trees 2 to 6 or 7 years old are apt to be attacked near the soil surface, and here is the place to look for the swelling upon young stock. (Fig. 1.) On trees several inches in diameter the disease is apt to work in a streak up and down the stem, in some cases checking the growth on the affected side of the tree, while at each side of this depressed streak a decided ridge is formed. Sometimes the affected part is killed, and then the action is similar to that of the white-pine blister rust upon the northern white pine, where old cankers are formed. On such old cankers of the pitch pines insects attack the affected bark and pitch oozes out, forming masses several inches across. (Fig. 2.) These masses are conspicuous, and, taken in connection with the ridged swelling of the stem and the thickened bark, they make one of the best field marks of the disease. There is a tendency toward an extra thickening and roughening of the bark

¹ The American forest trees are named according to Sudworth (49). Other trees and plants are named according to the American Joint Committee on Horticultural Nomenclature (4).

² Italic numbers in parentheses refer to Literature Cited, p. 19.

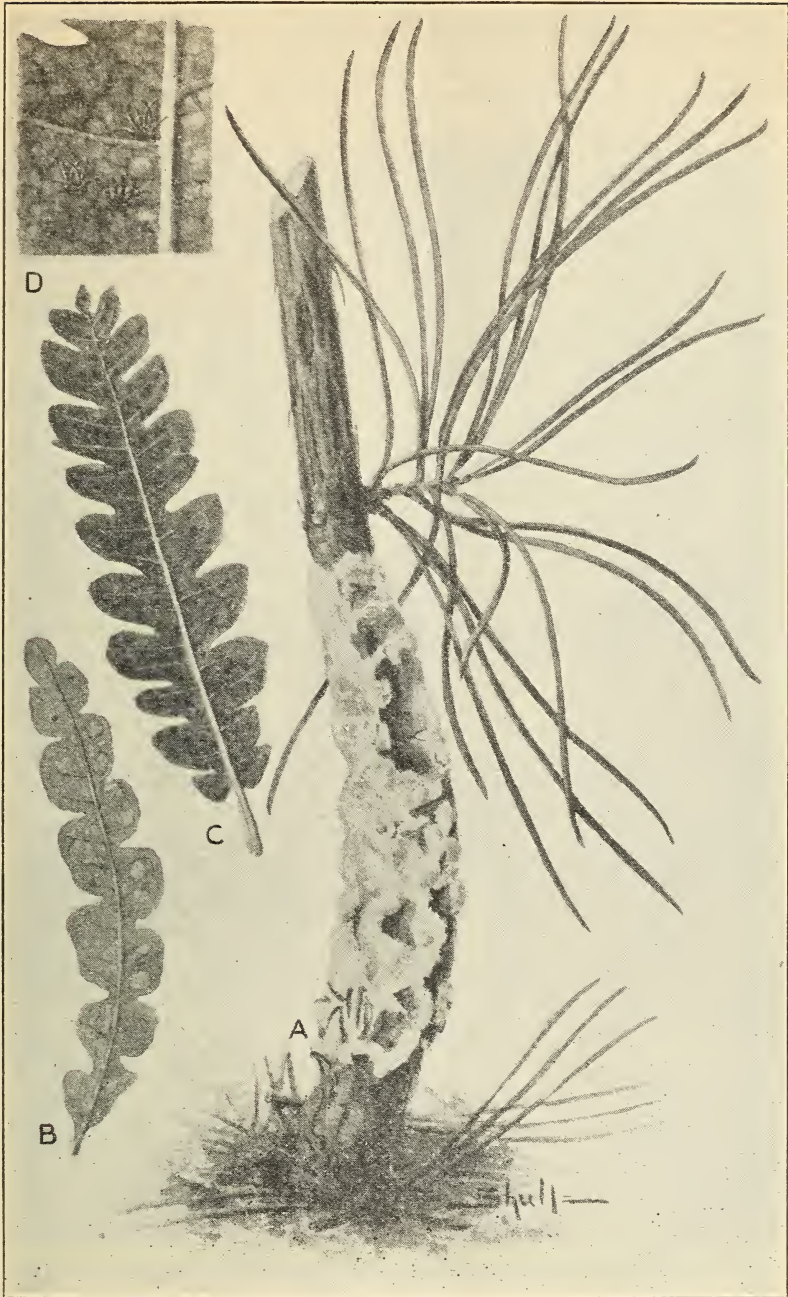


FIGURE 1.—Various spore stages of *Cronartium comptoniae*: A, Young stem of *Pinus rigida* heavily attacked and with abundant newly opened blisters; B, sweetfern leaf with early summer stage; C, sweetfern leaf with late summer stage; D, the same, slightly magnified. (A, B, C, natural size; D, $\times 2$)

on the affected spots on older trees. This alone is not striking, because of the normally rough, scaly bark of the pitch pines, but it often helps to indicate the presence of the disease.

When young trees of a species that sprouts readily are attacked, the normal, single-stemmed tree form may be changed to that of a



FIGURE 2.—Pitch exuding from diseased part of trunk of *Pinus rigida*, 4 inches diameter at breast height, badly cankered by *Cronartium comptoniae*. The lower branch on the left side shows swelling caused by the disease and remnants of the blisters, which are practically empty of spores. (Photograph by W. H. Snell)

multiple-stemmed shrub which is very abnormal in appearance. The blisters, either entire or broken, are the best symptom of this disease, but they are present only for about two or three weeks in the latter

part of May and early June. They can not be taken as indicating this disease with certainty, as there is a very similar blister rust of some of the pitch pines, *Cronartium pyriforme* (Peck) Hedgcock and Long,⁴ which is distinct from the sweetfern blister rust, and which in its alternate stage attacks several species of herbaceous plants of the genus *Comandra*. As stated elsewhere in this circular, the two rusts were confused for nearly 40 years. *Cronartium pyriforme* appears not to be so common in the Eastern States as is the sweetfern rust and is much less likely to be found by the untrained observer.

An attempt has been made to identify *Cronartium comptoniae* in early stages of its growth in pines by the characteristics of its mycelium (31). It was found that the characters were such that one might say confidently that one of the blister-rust fungi is present, but they were not distinctive enough to separate this particular species from *C. pyriforme*, which attacks some of the same species of pine and also produces similar cankers.

The alternate stage of the sweetfern blister rust grows on the leaves, flowers, and fruits of sweetfern and sweetgale, *Myrica gale* L. Like the white-pine blister rust, a close relative, it has two forms of spores on the alternate hosts. The first appears in June as orange-yellow powdery spots, varying in size from a pin point to one-fourth of an inch across, on the lower sides of the leaves, and occasionally on the inflorescence. (Fig. 1, B.) The later stage appears on the same parts of the plants from about July 1 to freezing weather in the fall, in the form of tufts of brownish stout hairs approximately one-fourth inch long. (Fig. 1, C.)

TREES AND SHRUBS ATTACKED

The sweetfern blister rust has been reported as occurring upon the following species of pitch pines, that is, pines that have their needles in bundles of 2 or 3 instead of 5.

Jack pine (*Pinus banksiana* Lambert), lodgepole pine (*P. contorta* Loudon), shortleaf pine (*P. echinata* Miller), Jeffrey pine (*P. jeffreyi* Oreg. Comm.), Swiss mountain pine (*P. montana* Miller), Austrian pine (*P. nigra* Arnold), western yellow pine (*P. ponderosa* Lawson), American mountain pine (*P. pungens* Lambert), Norway pine (*P. resinosa* Sol.), pitch pine (*P. rigida* Miller), Scotch pine (*P. sylvestris* L.), loblolly pine (*P. taeda* L.), and Virginia pine (*P. virginiana* Miller).

Like the white-pine blister rust, this one has an alternate stage of growth upon shrubs (sweetfern and sweetgale), which are common throughout the range of the native pines which it attacks. The sweetfern grows in dry, sterile soils where the poorer pitch pines are frequently found, while the sweetgale grows in swampy situations. Thus, between the two, there usually is an alternate host plant for the disease wherever the pitch pines grow in the Northern States and Canada. A third species of *Myrica*, the bayberry (*Myrica carolinensis* Miller) of the coast, especially northward from Maryland, has been inoculated successfully (51), but never has been found infected naturally. It is a possible third alternate host plant.

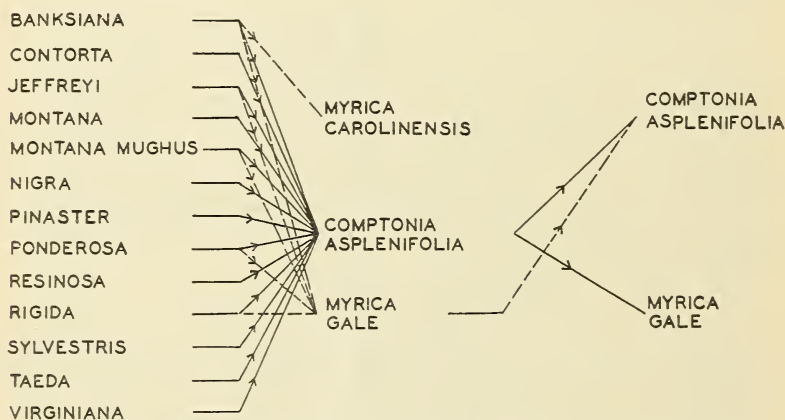
INOCULATIONS

When the senior writer began to work with *Cronartium comptoniae*, it was so inextricably confused with *C. pyriforme* that the only way

⁴ For a description of this fungus and the disease caused by it, see Hedgcock and Long (26).

to be certain of the identity of the fungus on pines was to inoculate it on the leaves of *Comptonia asplenifolia* or *Myrica gale*. Nearly all the specimens collected by the writers were thus identified. Many more inoculations were made than would normally be made. Table 1 gives the results of all the inoculations known to have been made upon *Comptonia asplenifolia*, *Myrica gale*, and *M. carolinensis*. Figure 3 shows between what hosts successful transfers have been made. There were no successful inoculations from *Myrica* to pines. Some years ago a number of such inoculations were made by the senior writer and his associates upon a number of the pitch pines. The conditions for infection were too poorly understood for intelligent work to be done, and no infections resulted, as might be expected under the circumstances.

PINUS

FIGURE 3.—Successful cross inoculations with *Cronartium comptoniae* on various hostsTABLE 1.—Inoculations of *Cronartium comptoniae* on different hosts
ON COMPTONIA ASPLENIFOLIA

Source of spores	Experimenters	Inoculations	
		Made	Successful
		Number	Number
Pinus banksiana.....	Clinton (16, rpt. 1914, p. 20), Lyman, Spaulding, Weir and Hubert (51).....	6	6
P. contorta.....	Hedgecock, Spaulding (47).....	3	3
P. jeffreyi.....	Spaulding.....	1	1
P. montana.....	do.....	1	1
P. montana mughus ¹	Lyman; Spaulding; Clinton and McCormick (17).....	5	5
P. nigra.....	Lyman; Clinton and McCormick (17), Spaulding (46, pt. 2).....	4	4
P. ponderosa.....	Clinton and McCormick (17), Gravatt; Hedgecock (46, pt. 2), Spaulding (46, pt. 1-2).....	9	9
P. resinosa.....	Spaulding.....	2	2
P. rigida.....	Clinton and McCormick (17), Hedgecock (46, pt. 3), Orton (1), Spaulding (46, pt. 3).....	11	11
P. sylvestris.....	Clinton (12, 13), Clinton and McCormick (17), Spaulding (46, pt. 1-2).....	6	6
P. taeda.....	Spaulding (46, pt. 1).....	1	1
P. virginiana.....	Orton (1).....	1	1
Comptonia asplenifolia.....	Hedgecock (46, pt. 3), Long (46, pt. 3), Spaulding (46, pt. 3).....	6	6
Myrica gale.....	Spaulding (46, pt. 3).....	2	2

¹ P. montana mugho (17).

TABLE 1.—Inoculations of *Cronartium comptoniae* on different hosts—Continued

Source of spores	Experimenters	Inoculations	
		Made	Successful
		Number	Number
<i>Pinus banksiana</i>	Lyman; Weir, and Hubert (51).....	2	2
<i>P. jeffreyi</i>	Gravatt.....	1	1
<i>P. montana mughus</i>	Lyman.....	2	2
<i>P. nigra</i>	do.....	1	0
<i>P. ponderosa</i>	Gravatt.....	1	1
<i>P. pungens</i>	Spaulding.....	1	1
<i>P. rigida</i>	Hedgecock, Spaulding.....	2	2
<i>Comptonia asplenifolia</i>	Spaulding (46, pt. 3).....	2	2

ON MYRICA CAROLINENSIS			
<i>Pinus banksiana</i>	Weir and Hubert (51).....	1	1
<i>P. jeffreyi</i>	Gravatt.....	1	0
<i>P. montana mughus</i>	Lyman.....	1	0
<i>P. nigra</i>	do.....	1	0
<i>P. ponderosa</i>	Gravatt.....	1	0
<i>P. rigida</i>	Gravatt, Hedgecock, Spaulding.....	3	0

Besides the inoculations included in Table 1, a considerable number were made by the senior writer on other species of *Myrica*. The species thus tested were: *M. californica* Cham., *M. cerifera* L., *M. inodora* Bartram, and *M. pumila* Michx. Each was tested several different times with spores from several pins that gave good infections on *Comptonia asplenifolia* and *Myrica gale* in parallel inoculations at the same time (46, pt. 3). The evidence shows that these species are not susceptible.

Arthur (6) made what was probably the first attempt to inoculate a species of *Myrica* with spores of this fungus. His attempt, however, was made upon *M. cerifera*, which has never yet been infected by this fungus.

Attempts have also been made to inoculate plants known to be hosts for other blister rusts, with spores of *Cronartium comptoniae*. Such tests were made by Clinton (13) upon *Solidago* and *Quercus*. Hedgecock⁵ tested *Quercus borealis* Michx. Orton tested three species of *Quercus* (1). Weir and Hubert (51) tested *Castilleja angustifolia* (Nutt.) G. Don, *C. mineata* Benthams, and *Quercus borealis*. Still more recently Clinton and McCormick (17) tested *Ribes nigrum* L., *R. vulgare* Lam., and *Quercus alba* L. All these experiments failed to give infections.

In the same way *Cronartium pyriforme* has been tested upon *Comptonia asplenifolia*, but without yielding infections (26). In Europe Klebahn (35) tried unsuccessfully to inoculate sweetfern and sweetgale with spores of *Cronartium asclepiadeum*.

DISTRIBUTION IN NORTH AMERICA

Cronartium comptoniae is a North American fungus, which, so far as is known, is strictly limited to the so-called pitch pines, but it appears to affect all the species. It seems to be quite clear-cut in

⁵ Unpublished work.

distribution, as it has not yet been spread by man to many new localities. Jack pine and sweetfern seem to be its favorite hosts, and the range of the fungus largely coincides with that of these two hosts. Unless care is taken in the shipment of pitch-pine nursery stock this range will be extended, possibly with locally disastrous results. Several species of *Myrica* are native in the Rocky Mountain and Pacific coast regions; should any of them prove susceptible, its introduction there might be ominous for some of the western pitch pines, which are already known to be especially susceptible to it. It might even become a decisive local factor in their growth and reproduction. The danger from shipping infected pitch-pine stock to western points can not be correctly estimated, as it is a real danger of unknown proportions and possibilities. Too little is known of its readiness to attack pines from without its range. They should be used with caution in the East until their reaction to it is well established.

The known distribution of this fungus and the disease caused by it is as follows:

CANADA

NOVA SCOTIA:

Myrica gale.—Pictou (F. P. 2858⁶; Arthur herb.⁷; 24, 25).

NEW BRUNSWICK:

Pinus banksiana.—Northumberland district (F. P. 24041).

QUEBEC:

Pinus sylvestris.—Grand Mere (53).

ONTARIO:

Comptonia asplenifolia.—Fonthill (F. P. 24044); Timagami Forest Reserve (Dominion of Canada botanist herb.); (37).

Myrica gale.—Kalmar (Dearness herb.); Kenora (10); north of Lake of the Woods (Seymour, A. B. and Earle, F. S. Economic fungi, 216); Spanish River north of Georgian Bay (Dearness notes); Timagami Forest Reserve (Dominion of Canada botanist herb.); (37).

Pinus sp.—Kenora (10).

MANITOBA:

Pinus banksiana.—Lake Winnipeg (Weir herb.).

SASKATCHEWAN:

Pinus banksiana.—Northern part (Weir herb.).

BRITISH COLUMBIA:

Myrica gale.—Chee Kye (36); Daisy Lake⁸ (F. P. 40302); Hidden Lake (36); North Vancouver (36); Pemberton (36); Pender Harbor (36); Squamish (36); Starvation Lake (36).

Pinus contorta.—Daisy Lake⁹; Lake Lucile (Bureau of Plant Industry, pathological collections); Starvation Lake (36).

UNITED STATES

MAINE:

Comptonia asplenifolia.—Kittery (F. P. 24047).

Myrica gale.—Orono (Ellis, J. B. North American Fungi, 1055. Ellis, J. B., and Everhart, B. M. Fungi Columbiana, 1482.) (43).

Pinus banksiana.—Brunswick (F. P. 32517); Denmark (F. P. 45337).

Pinus resinosa.—Hiram (F. P. 37302).

Pinus rigida.—Poland¹⁰; Welchville (F. P. 51014).

Pinus sylvestris.—Alfred (F. P. 51639).

⁶ The letters F. P. followed by a number refer to a specimen in the Division of Forest Pathology bearing the collection number mentioned.

⁷ "Herb." is an abbreviation for herbarium.

⁸ MARTIN, G. H. DISEASES OF FOREST AND SHADE TREES, ORNAMENTAL AND MISCELLANEOUS PLANTS IN THE UNITED STATES IN 1924. U. S. Dept. Agr., Bur. Plant Indus., Plant Disease Rptr. Sup. 42: 323-325, 371. 1925. [Mimeographed.]

⁹ MARTIN, G. H. DISEASES OF FOREST AND SHADE TREES, ORNAMENTAL AND MISCELLANEOUS PLANTS IN THE UNITED STATES IN 1926. U. S. Dept. Agr., Bur. Plant Indus., Plant Disease Rptr. Sup. 55: 339. 1927. [Mimeographed.]

¹⁰ UNITED STATES DEPARTMENT OF AGRICULTURE, BUREAU OF PLANT INDUSTRY. NOTES FROM MAINE. U. S. Dept. Agr., Bur. Plant Indus., Blister Rust News 9 (6): 4. 1925. [Mimeographed.]

NEW HAMPSHIRE:

Comptonia asplenifolia.—Chocorua (Farlow herb.); Concord (F. P. 2531, 2739); Franklin (F. P. 51771); Hinsdale (F. P. 2542); Nashua (F. P. 2530); North Conway (F. P. 24039, 37122, 37261; 40); Shelburne (Reliquiae Farlowianae, 217); Wakefield (F. P. 45341); West Concord (F. P. 2830).

Myrica gale.—North Conway (F. P. 37121).

Pinus banksiana.—Dover (F. P. 23749).

Pinus contorta.—Durham (F. P. 20686).¹¹

Pinus coulteri.—Durham (N. H. Agr. Exp. Sta. herb.).

Pinus montana mughus.—Concord (F. P. 20691).

Pinus ponderosa.—Durham (F. P. 20685).

Pinus resinosa.—Durham (F. P. 20687).

Pinus rigida.—Chichester (F. P. 45344); North Conway (F. P. 24024, 37106; 40); Wakefield (F. P. 45343).

Pinus sylvestris.—Freedom (F. P. 16127); Gerrish (F. P. 2675); Keene (Hahn's notes).

VERMONT:

Comptonia asplenifolia.—Burlington¹² (F. P. 2836; 39, 48); Fort Ethan Allen (Univ. Vt. herb.); Weathersfield (F. P. 24040; 48).

Pinus contorta.—Burlington.¹²

Pinus nigra.—Essex Junction (F. P. 37283).

Pinus ponderosa.—Burlington (F. P. 37123; 48).

Pinus resinosa.—Burlington;¹² Essex Junction (F. P. 37285).

Pinus rigida.—Burlington (F. P. 2753; 48); Essex Junction (F. P. 17709, 37284; 27, 48); Rockingham (F. P. 37286).

Pinus sylvestris.—Burlington¹² (F. P. 20664, 37112; 48); Essex Junction (F. P. 37282); Jamaica (F. P. 37291).

CONNECTICUT:

Comptonia asplenifolia.—Granby (F. P. 34550; Farlow herb.); Ledyard (Bureau of Plant Industry pathological collections); Plainfield (Bartholomew, E., North American Uredinales, 2207); Plainville (Seymour, A. B., and Earle, F. S., Economic Fungi, 217); Rainbow (13); Storrs (Farlow herb.; Arthur herb.; 6, 13); Union (Farlow herb.).

Pinus banksiana.—Rainbow (16, rpt. 1914, p. 20).

Pinus contorta.—Coscob.¹³

Pinus maritima.—Rainbow (15, 29).

Pinus montana.—Rainbow (F. P. 23709; 16, rpt. 1913, p. 29).

Pinus murrayana.—Rainbow (29).

Pinus nigra.—Cheshire (F. P. 37303); Rainbow (F. P. 2835; 15, 28); Woodmont.¹⁴

Pinus ponderosa.—Rainbow (F. P. 2650, 2767, 23708; 16, 23, 28, 29).

Pinus rigida.—East Granby (F. P. 2768); Rainbow (15, 16, 28); Storrs (Arthur herb.; 6, 13).

Pinus sylvestris.—Cheshire (Hahn's notes); Mount Carmel;¹² Rainbow (F. P. 23710; Farlow herb.; 9, 14, 28, 29); Union (13); Wallingford (Weir herb., 473); Windsor (F. P. 2752).

RHODE ISLAND:

Comptonia asplenifolia.—East Providence (F. P. 20681); Johnston (F. P. 45339); Providence (F. P. 32674); Warwick (F. P. 2773, 45340).

Pinus montana mughus.—Cranston (F. P. 23824).

Pinus ponderosa.—Providence (F. P. 34549).

Pinus rigida.—Charlestown (F. P. 34666); East Providence (F. P. 20665); Warwick (F. P. 2772).

MASSACHUSETTS:

Comptonia asplenifolia.—Eastham (F. P. 51908); Mashpee (F. P. 51906); Monson (Farlow herb.); Newton (Ellis, J. B., North American Fungi, 285, 2081); Osterville (Farlow herb.); Sandwich (F. P. 51909); Springfield (F. P. 2595); Truro (F. P. 51907); Woods Hole (Farlow herb.).

¹¹ MARTIN, G. H. DISEASES OF FOREST AND SHADE TREES, ORNAMENTAL AND MISCELLANEOUS PLANTS IN THE UNITED STATES IN 1921. U. S. Dept. Agr., Bur. Plant Indus., Plant Disease Rprtr. Sup. 23: 432-435, 437-438, 445. 1922. [Mimeographed.]

¹² See footnote 8.

¹³ MARTIN, G. H. DISEASES OF FOREST AND SHADE TREES, ORNAMENTAL AND MISCELLANEOUS PLANTS IN THE UNITED STATES IN 1923. U. S. Dept. Agr., Bur. Plant Indus., Plant Disease Rprtr. Sup. 29: 399, 1923. [Mimeographed.]

¹⁴ See footnote 8.

MASSACHUSETTS—Continued.

Pinus contorta.—Topsfield (F. P. 20669).

Pinus jeffreyi.—Topsfield (F. P. 20650).

Pinus montana mughus.—Dedham (F. P. 2670); North Abington (F. P. 2669).

Pinus nigra.—Bedford (F. P. 2779).

Pinus ponderosa.—Bedford (F. P. 2777); Hamilton (F. P. 45815); Jamaica Plain (Farlow herb.; 2); North Abington (F. P. 2524); Petersham (F. P. 2844, 2778, 8370); Topsfield (F. P. 20649).

Pinus rigida.—East Brookfield (F. P. 16798); Framingham (F. P. 2780); Hathorne (F. P. 2671); Haverhill (F. P. 37368); Montague (F. P. 37363); Seekonk (F. P. 37107); Sheffield (F. P. 16105); Turners Falls (F. P. 45818); Westfield (F. P. 45816).

Pinus sylvestris.—Bridgewater (F. P. 22403); Framingham (F. P. 2781); Hyde Park (F. P. 20684); Marthas Vineyard (F. P. 51641); North Abington (F. P. 2525); Petersham (Spaulding's notes); Westfield (F. P. 16800); Winchendon (F. P. 37304).

Pinus sylvestris rigensis Loud.—Leverett (F. P. 51539).

NEW YORK:

Comptonia asplenifolia.—Ashokan (F. P. 23314); Bluff Point (Spaulding's notes); (Bartholomew, E., North American Uredinales, 3408); Central Islip (30); Glens Falls (Spaulding's notes); Hicksville (N. Y. Bot. Garden herb.); Keeseville (F. P. 25318); Long Island (Ellis, J. B., North American Fungi, 1052; 41); Wading River (N. Y. State Mus. herb.).

Pinus banksiana.—Wilmington (F. P. 37109).

Pinus jeffreyi.—Westbury (F. P. 17828).

Pinus montana.—Bluff Point (F. P. 23837).

Pinus montana mughus.—Hicksville (F. P. 23836); Rhinebeck (F. P. 51640).

Pinus nigra.—Bluff Point (F. P. 2676, 23838); Patchogue (F. P. 51015).

Pinus ponderosa.—Ashokan (F. P. 23313); Bluff Point (F. P. 2677); Westbury (F. P. 2824).

Pinus resinosa.—Bluff Point (Spaulding's notes).

Pinus rigida.—Albany (9); Bluff Point (F. P. 2678); Glens Falls (F. P. 1257, 2754; Arthur herb.; N. Y. State Mus. herb.); Gloversville (Arthur herb.; N. Y. State Mus. herb.); Hudson Falls (Arthur herb.; N. Y. State Mus. herb.; 9); Keeseville (F. P. 25317, 37213); Port Kent (F. P. 45637, 45817); Pottersville (F. P. 37275); Southold (11).

Pinus sylvestris.—Bluff Point (F. P. 2822; 9); Ithaca (F. P. 32494); Woodgate (F. P. 16799; 54).

NEW JERSEY:

Comptonia asplenifolia.—Belleplain (Ellis, J. B., and Everhart, B. M., Fungi Columbiana, 1724); Buena (F. P. 15671); Clayton (F. P. 15674); Egg Harbor (Arthur herb.); Malaga (F. P. 22773); Mount Calvary (F. P. 22628, 38434); Newfield (F. P. 15662, 17959); New Gretna (F. P. 2662; Arthur herb.); Toms River (Arthur herb.; N. Y. Bot. Gard. herb.); Waterford (Arthur herb.).

Pinus banksiana.—Mays Landing (F. P. 2666).

Pinus nigra.—Gladstone (F. P. 22183); Morristown (F. P. 22140).

Pinus rigida.—Belleplain (F. P. 20690); Clayton (F. P. 15673); Mount Calvary (F. P. 24517); Newfield (Arthur herb.; 9).

Pinus sylvestris.—Mays Landing (F. P. 2665); West Englewood (F. P. 3339).

Pinus taeda.—Burlington;¹⁵ New Gretna (F. P. 2660, 2776, 3475, 16999).

Pinus virginiana.—Lakehurst (1); Newfield (Ellis, J. B., North American Fungi, 1021; 7).

PENNSYLVANIA:¹⁶

Comptonia asplenifolia.—Bartonsville (F. P. 43359); Caledonia (F. P. 17922); Petersburg (F. P. 15644); Reading (Arthur herb.).

Pinus contorta.—Caledonia (F. P. 15399).

Pinus densiflora.—Caledonia (1).

Pinus echinata.—Bear Meadows (38).

Pinus nigra.—Caledonia (F. P. 15398, 17796, 37214).

Pinus ponderosa.—Colmanville (F. P. 9978); Greenwood Forest (F. P. 22088); Reading (Arthur herb.; 1); Stone Valley (1).

¹⁴ See footnote 8.

¹⁶ Kern, Thurston, Orton, and Adams (34) list these hosts for Pennsylvania, but give no localities of occurrence.

PENNSYLVANIA—Continued.

Pinus pungens.—Greenwood Forest (F. P. 22089).

Pinus rigida.—Bear Meadows (1); Caldwell;¹⁷ Petersburg (F. P. 15484).

Pinus virginiana.—Charter Oak (Arthur herb.); State College (3); Stone Valley¹⁹ (1).

MARYLAND:

Pinus rigida.—Admiral (1).

Pinus virginiana.—Naval Academy Junction (F. P. 2938).

VIRGINIA:

Comptonia asplenifolia.—Blacksburg (Arthur herb.).

NORTH CAROLINA:

Comptonia asplenifolia.—Location unknown (19); Hillsboro (Brit. Mus. Nat. Hist. herb.).

Pinus echinata.—Biltmore (F. P. 1597).

OHIO:

Pinus nigra.—Cincinnati (F. P. 18199, 18200, 18204; 42); Wooster (F. P. 18196, 18201; 42).

Pinus montana.—Wooster (F. P. 2680).

Pinus ponderosa.—Cincinnati (F. P. 34548).

Pinus sylvestris.—Location unknown.^{18 19}

INDIANA:

Pinus nigra.—Michigan City (Weir herb.).

MICHIGAN:

Comptonia asplenifolia.—East Tawas (F. P. 2684); Roscommon (F. P. 30008; Arthur herb.; 18, 32, 33, 44, 45).

Pinus sp.—Grand Rapids (Mich. Agr. Col. herb.; 18).

Pinus banksiana.—Bay City (Weir herb. 480); East Tawas (F. P. 2683; Weir herb. 475, 479, 9564); Marquette (Weir herb. 474); Racoon (Weir herb. 470, 481).

Pinus contorta.—Roscommon (F. P. 2827, 12466; 18, 27, 32, 33, 44).

Pinus echinata.—Detroit (Weir herb. 462).

Pinus nigra.—Roscommon (F. P. 2826, 2828, 22121; 32, 33, 44).

Pinus ponderosa.—Racoon (F. P. 25022); Roscommon (F. P. 2829, 22122; 32).

Pinus sylvestris.—Roscommon (F. P. 2623, 22123, 30004).

WISCONSIN:

Comptonia asplenifolia.—Gordon (Arthur herb.; 20); Mosinee (Davis, J. J. Fungi Wis. Exsicc. No. 86); Phillips (F. P. 2736); Spooner (Arthur herb.; Vestergren, *Micromycetes rariores selectii* No. 1651); Trout Lake (F. P. 2686, 2825).

Pinus banksiana.—Adams County (21, pt. 5); Douglas County (21, pt. 3); Gurney (Weir herb. 472); Juneau County (21, pt. 5); Millston (21, pt. 5); Solon Springs (Weir herb. 476); Trout Lake (F. P. 2688); Vilas County (21, pt. 3); Winneboujou (Weir herb. 477).

Pinus nigra.—Trout Lake (F. P. 24376; 21, pt. 5).

Pinus ponderosa.—Trout Lake (F. P. 2687).

Pinus sylvestris.—Trout Lake (F. P. 24326, 24377).

MINNESOTA:

Comptonia asplenifolia.—Cloquet (F. P. 18103; Minn. Agr. Expt. Sta. herb.).

Pinus banksiana.—Carlton County;²⁰ Cass Lake (F. P. 18048, 18056; Weir herb. 471); Cloquet (F. P. 18102, 39220; Minn. Agr. Expt. Sta. herb.; 52); Ely (Weir herb. 469); Kimberly (F. P. 20692).

Pinus ponderosa.—Cloquet (Minn. Agr. Expt. Sta. herb.).

MISSOURI:

Pinus sylvestris.—St. Louis (Arthur herb.).

WASHINGTON:

Myrica gale.—Ilwaco (36).

Pinus contorta.—Ilwaco (36).

¹⁷ See footnote 8.

¹⁸ See footnote 11.

¹⁹ MARTIN, G. H. DISEASES OF FOREST TREES, ORNAMENTALS, AND MISCELLANEOUS PLANTS IN THE UNITED STATES IN 1920. U. S. Dept. Agr., Bur. Plant Indus., Plant Disease Rptr. Sup. 11: 297. 1920. [Mimeographed.]

²⁰ MARTIN, G. H. DISEASES OF FOREST AND SHADE TREES, ORNAMENTAL AND MISCELLANEOUS PLANTS IN THE UNITED STATES IN 1925. U. S. Dept. Agr., Bur. Plant Indus., Plant Disease Rptr. Sup. 50: 422. 1926. [Mimeographed.]

The distribution of the disease is given as specifically as possible so that the location of new nurseries may be made with complete knowledge of disease possibilities in each specific locality. In general, it can be stated that it is found in all extensive areas of sand within the glaciated region. Figures 4 and 5 show its distribution in eastern North America and in the recently discovered area of the Northwest and British Columbia. It is evidently present in the intervening Canadian Provinces, probably well northward in the range of the jack and lodgepole pines.

ECONOMIC IMPORTANCE

The damage done by *Cronartium comptoniae* to the attacked tree is largely due to its girdling action. The smaller the tree the more

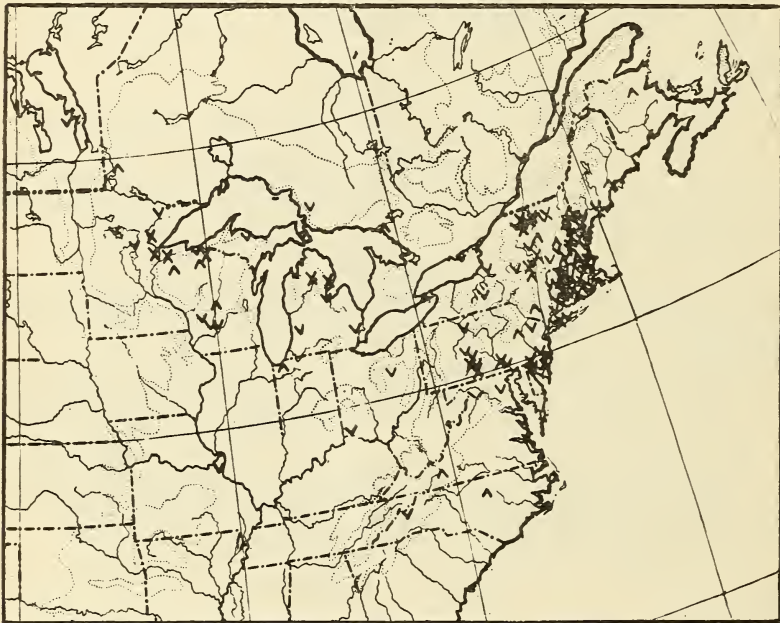


FIGURE 4.—Known distribution of *Cronartium comptoniae* in eastern North America. ∇ Indicates the disease on pines; Δ, the disease on *Comptonia* and *Myrica*; X, both stages of the disease in the same locality

apt it is to be entirely girdled and killed. After a diseased tree has attained a diameter at the base of about 3 inches it is relatively safe, although even then it may be crippled and finally broken over by snow. Partly girdled trees also are much more apt to die from drought than are healthy ones; in this respect the disease accentuates the lack of needed water, just as the white-pine blister rust does.

In 1912 the senior writer began annual observations of an area of approximately 2.75 acres of natural reproduction of pitch pine, *Pinus rigida*, near Glens Falls, N. Y., where this disease was quite evenly distributed. These observations extended to 1921 annually, with additional observations in 1924. This was done to get some information as to the annual mortality from this disease with one of our

native species of pines that is not considered to be much injured by it. During the period covered some new seedlings appeared within the area, although these were not numerous. In 1912 the stand was rather broken; the largest trees then were about 10 feet tall, with a few about 20 feet high, and the majority were not over 6 feet tall. Sweetfern was present in small openings in the stand and entirely covered the ground for 100 yards or more along one side. None of the trees was over 100 feet from sweetfern. In 1924 there was practically a full stand, and there were 2,748 living trees on the area. Mortality has been limited almost without exception to the diseased trees. Two hundred and twenty-six trees died during the period. The number of visibly diseased trees present on the area at any single time varied from 147 to 202. An effort was made to keep

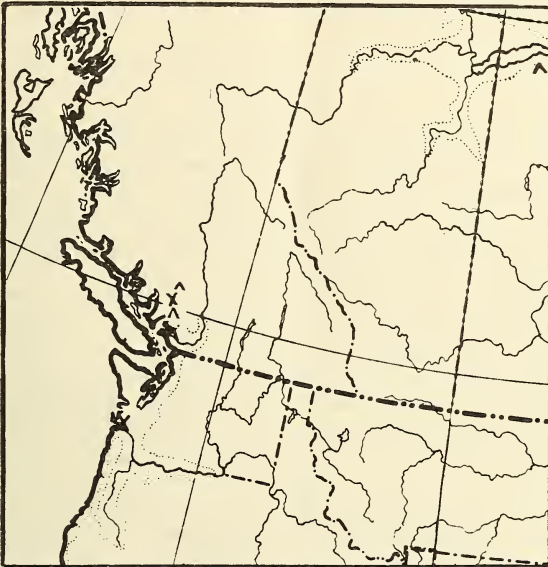


FIGURE 5.—Known distribution of *Cronartium comptoniae* in western North America. Δ Indicates the disease on *Comptonia* and *Myrica*; \times , both stages of the disease in the same locality

metal tags on all of the diseased trees but with indifferent success because of the activity of irresponsible persons traversing the area. Table 2 shows the mortality.

TABLE 2.—Mortality of trees of *Pinus rigida* attacked by *Cronartium comptoniae*, near Glens Falls, N. Y., 1912–1924

Year	Trees diseased	Trees dead	Year	Trees diseased	Trees dead
1912.....	147	8	1918.....	162	8
1913.....	184	10	1919.....	188	19
1914.....	71	11	1920.....	149	33
1915.....	191	9	1921.....	174	39
1916.....	202	11	1924.....	198	62
1917.....	176	16	Total.....		226

The total number of visibly diseased trees has varied considerably. This variation is due in most part to the fact that observations were made too late in the season so that all diseased trees could not be recognized. The years 1919 to 1924 show much greater mortality than do the earlier years. Probably this is due to increased competition, as the stand has largely closed during the period and has about doubled in height. If considered on a basis of percentage of mortality of diseased trees, the loss is rather heavy. Considering the trees of the area as a stand, in spite of the fact that there have been small patches where the disease took nearly every tree, the remaining trees have filled the openings so that one can not say that any material damage has been done to the stand as a whole, except that there undoubtedly has been a slowing up in total growth due to the replacing of the dead older trees by younger trees. Whether this blister rust attacks the most vigorous trees of a stand is uncertain, as diseased trees are commonly so heavily attacked at first as to make it uncertain whether slowing of growth may not be due to the fungus rather than preceding its attack. The killing by the disease has also acted as a natural thinning needed in some parts as the stand became crowded. Probably the most serious damage from the disease in pitch pines native to its range is the killing off of young seedlings, thus delaying reproduction or making it very spotty. In natural reproduction of Virginia pine in Stone Valley, Pa., Overholts found 22½ per cent of the trees in a stand ranging in age up to 30 years infected.²¹

In nurseries the loss of seedlings has been as high as 5, 10, and even 20 per cent with single species of the pitch pines. Such a loss is serious, and to it must be added the cost of trying to sort out all diseased seedlings, with more or less indifferent success. With a commercial nursery this has the further adverse effect of shaking public confidence in its stock when an occasional diseased tree is found in a shipment, as is apt to be the case. The shipment of nursery stock for long distances into another region differing in climate and in native tree species has very uncertain significance for the future. Untested species of *Myrica* which are quite widely distributed in North America may prove to be susceptible to this fungus. Should this happen, the possibilities for local damage might be far greater than is now suspected.

The greatest loss from this disease has occurred in plantations, although the initial infection in most cases has taken place in the nursery before the trees were planted in the field. The two western pines, *Pinus contorta* and *P. ponderosa*, which have been planted to some extent east of the Mississippi Valley well beyond their native range, have in several instances been heavily infected. In the case already mentioned in Michigan the loss was practically total (33, 44, 45). In Connecticut *P. ponderosa* has suffered a loss of 45 per cent from this disease "and drought" (23, 28). It seems peculiar that this species, which normally grows in a region with small rainfall, should suffer very much from drought anywhere in the Northeast. In a few instances rather heavy damage has been reported to occur on *P. sylvestris*, although this is not usual. *P. taeda* has been mentioned as

²¹ See footnote 11.

menaced by this disease in New Jersey plantations. Other species of pitch pines are planted only in small numbers, so that little is known of their reaction toward this fungus.

With the campaign to increase greatly our forestry planting program definitely under way, the use of the pitch pines is also certain to increase greatly. As new nurseries are established, much care should be taken to locate them as far as possible from extensive areas of the alternate hosts of this and other closely related parasitic fungi of young forest trees. While this fungus is quite ready to attack any of the pitch pines, relatively little is really known about the danger to the different species. As planting increases, unusual species should be used cautiously and only on an experimental basis until more is known about them. It is significant that all American pitch pines that are native to regions distant from the native range of this fungus are susceptible to attack whenever exposed to it.

THE PARASITIC FUNGUS

SYNONOMY

The fungus under consideration has for a long time been confused with other closely related species of *Peridermium* (7). As stated by Hedgcock and Long (26), it was confused with *Peridermium pyriforme* Peck, which also grows on various species of the pitch pines. *P. pyriforme* was named in 1875, relatively early in the history of pathology. While the spores of *P. pyriforme* are quite characteristic, this fact was either ignored or the spores were not carefully examined when specimens were named. In 1913 Arthur and Kern (8) announced that *P. pyriforme* is a good and distinct species. At about the same time Hedgcock and Long examined specimens of a fungus that agreed with the characters stated by Peck to differentiate his new species *P. pyriforme*. In 1914 Orton and Adams (38) named the sweetfern fungus *Peridermium comptoniae*, this being the first time it had a name of its own.

The alternate stage of the sweetfern fungus fared a little better. In 1906 Arthur named it *Cronartium comptoniae* (5). Previously it had gone by the name *Cronartium asclepiadeum* (Willd.) Fries, and it was supposed to be the same as this European species. While some have believed that the North American *C. comptoniae* may be identical with *C. asclepiadeum* of Europe, this does not now seem likely. Several years ago Klebahn (35) tried to inoculate the European fungus onto the sweetfern, but without success. This would indicate that this plant is not a host for the European fungus. He also tried to inoculate the pine stage of *C. asclepiadeum* onto *Myrica gale*, but without success, indicating that this too is not a host for the European fungus. So far as known to the writers, no tests in the reverse direction have been made with the American sweetfern blister rust upon the hosts of the European rust. Such tests would help to make more certain the real status of the two fungi.

Until 1908 it was not definitely known that the *Peridermium* was a stage of the rust upon *Comptonia* and *Myrica*. Clinton in that year successfully inoculated *Comptonia asplenifolia* with *Peridermium* spores from *Pinus sylvestris*, obtaining *Cronartium comptoniae* upon the infected leaves (12, 13). This connection had been suspected but never proved. Since then a number of different workers have

repeatedly made similar inoculations. The fungus in both stages is now known by the name *Cronartium comptoniae*. Because of the known presence of *C. pyriforme* in part of the same territory and on some of the same species of pitch pines, it is necessary to use a common name which is rather long. Sweetfern blister rust is perhaps as good a common name as can be found under the circumstances.

LIFE HISTORY

While the life history of this fungus is far from completely worked out, some of the main features may be indicated. Infection of young seedlings becomes evident usually in their third year. The pycnia must be formed early in their second year, as they are definitely known to precede the aecia (2, 3, 52). The aecia appear in the third year, although there may be a few precocious cases where they form on 2-year-old wood, as is done occasionally by the white-pine blister rust. Usually there is but little swelling of the affected stems, the blisters of the aecia being the main symptom of the disease at first. If the tree lives for several years with the disease there is more pronounced deformation and irregular swelling in the shape of ridges running up and down the stem. The aeciospores are freely blown about by the wind, as shown by observations in the field (46, pt. 1). The sporidia of this blister rust are so similar to those of the white-pine blister rust that the conditions for their survival and germination are probably very much the same. The pitch pines and the sweetfern inhabit localities that are typically sandy and sterile. Except during cloudy weather or storms the air is dry, and it dries quickly after a storm. The chances for infection in places where the fungus occurs naturally are minimized by this dryness of the air. During the warm months, however, showers are apt to fall, especially in the afternoon in the latter part of summer and early fall, when the teliospores are matured and are ready to infect pines in their vicinity.

When an aeciospore lodges on the lower surface of a leaf of sweetfern or sweetgale, it germinates promptly if there is some water present. Free water is necessary, as inoculation experiments plainly show. Infections can be quite certainly made if the surrounding air is moist enough, and tests made for the purpose show that without water none will result. The infection by an aeciospore must develop for 8 to 12 days, after which time mature uredinia form under favorable conditions. These appear as small orange-yellow pustules commonly scattered thinly over the lower surface of the leaf. These urediniospores in turn may infect more *Comptonia* and *Myrica* leaves and produce more uredinia. After an interval of about 30 days the uredinial spots produce a second type of fruiting body called the telia. These are slender brownish filaments up to about one-fourth of an inch in length, growing out at right angles from the lower surface of the leaf. The urediniospores are readily blown about, but they appear to serve only as local intensifiers of the disease on *Comptonia* and *Myrica*. They can not infect pines, so far as is now known.

The telia germinate without being distributed from the parent leaf. When they germinate small rounded spores are formed, which in turn are readily distributed by the wind. These are blown to pitch-pine leaves and there may start infection of the pine, to develop new pycnia and aecia.

DISSEMINATION

The agents that disseminate the spores of *Cronartium comptoniae* and the distance that these spores can be carried and still be capable of causing the disease are two most important problems in the life history of this fungus for one who is to undertake its control or prevent its undue spread into new regions.

The aeciospores are known to be blown by wind and to cause infection of *Comptonia* or *Myrica* leaves for short distances (46, pt. 1). In one case the distance from rusted pines to *Comptonia* was less than 50 feet; in another case the infection on *Comptonia* leaves began a few feet from the pine and extended about 10 yards away in a fan-shaped area, showing very plainly that the aeciospores were carried by wind. In numerous instances *Myrica* leaves have been found infected near rusted pines, the infection becoming more and more scattered with the increase in distance from the pine furnishing the infecting aeciospores. Nothing is known concerning the maximum distance of dispersal of the aeciospores. If they are similar to the aeciospores of *Cronartium ribicola* in this respect, which seems likely, they may be blown long distances and still produce the disease on the leaves of *Comptonia* or *Myrica*. The climatic conditions under which *Comptonia asplenifolia* occurs are so favorable for desiccation, except in stormy weather, that such spores can survive but a relatively short time. In fact the writers believe the dryness of the air is the chief controlling factor in the local spread of this disease. These spores are perfectly adapted to dispersal by mammals, insects, and other animals, and there is good reason to believe that they can be dispersed by such agents locally.

No study of the dispersal of the uredospores has been made. They probably have a short "effective" dispersal distance and serve only as local intensifiers of the disease.

The sporidia are undoubtedly largely distributed by wind, although various animals may act as carriers. A few observations show that the sporidia may be blown a considerable distance from their source and cause infection of pitch pines, especially where there are large areas of ground, covered with sweetfern, over which the wind sweeps. In the case of the Michigan State Forest Nursery at Roscommon the nursery area was merely a patch of cultivated ground in the midst of an extensive area of sweetfern. At the time of the outbreak there on western pines (33, 44, 45) probably no part of the nursery was more than 150 yards distant from the *Comptonia*. With natural infection from jack pine to the sweetfern for many miles around, it is not at all surprising that many viable sporidia were swept by the wind into and over the nursery. In another nursery the sweetfern causing serious infection of pitch pines was some 100 or more yards distant and was located back of a screen of hardwood trees 40 to 50 feet tall. But the sweetfern area extended for miles on a sandy plain along which the wind swept. In this case the sporidia were swept up into the air in tremendous quantities and dropped over the tree screen into the nursery in an air eddy, causing considerable infection of pines.

In another instance the writers could find no *Comptonia* or *Myrica* within several hundred yards of an infected nursery, although *Comptonia* was present on a rocky ridge some distance away. Wind blowing over the ridge and thence to the nursery apparently must have

carried these sporidia alive for this distance, as infection was rather serious. Under very favorable weather conditions the sporidia probably may be carried for several hundred yards and cause infection of the more susceptible species of pitch pines. Other cases that bear out this conclusion have been seen.

Experience indicates that it is dangerous to establish a nursery for growing pitch pines within a mile of an extensive area of sweetfern or of sweetgale. Under such conditions, when the weather is favorable for their production, the sporidia are produced and float in an invisible cloud over the entire area. Naturally some of them are carried even by gentle winds for long distances, and resulting serious infection is scattered much farther than when the source of infection is small or the weather continues favorable but a short time.

PREVENTION AND CONTROL

The sweetfern blister rust can be prevented in nurseries by locating them at a considerable distance from waste land where sweetfern is growing in great quantities, and also where the nurseries are well separated from swamps in which sweetgale grows. A distance of one-fourth of a mile ought to be enough unless there are extensive areas of these alternate host plants. Where this is the case, a mile ought to separate the nursery from extensive waste lands where either of these shrubs grow abundantly. The general direction of the wind during rains and the lay of the land in the vicinity are important factors to be considered before establishing new nurseries (50).

Where infection occurs in a nursery, the seedling beds 1 and 2 years old should be protected by spraying the seedlings thoroughly with standard Bordeaux mixture or lime sulphur. It is possible that a dust spray might be efficient. Heavy rains will necessitate respraying, as the purpose is to maintain on the tender leaves a coating that is poisonous to the germinating spores of the fungus. Spraying probably should begin the latter part of July or early in August, when the earliest telia of the fungus are formed. It is believed that most of the infection takes place in the first two or three years of the seedlings' life, in the nursery, while the young plants are massed thickly in the seed beds and consequently do not dry out quickly after rains.

In plantings of infected pines it may be possible to cut out diseased branches where infection occurs on them instead of on the main stem. This has been done in at least one instance (14). In some instances it may pay to destroy all diseased young native pitch-pine trees found in an area around a nursery, to prevent heavy outbreaks on sweetfern within the area. Recently some experiments have been started to exterminate sweetfern by spraying with chemicals (54). This may prove to be a feasible method of getting rid of this host near nurseries.

SUMMARY

The sweetfern blister rust of pitch pines attacks many of the 2 and 3 leaved pines; also it has an alternate stage of growth on the shrubs known as sweetfern and sweetgale. It is widely distributed from Virginia and the Lake States northward, also in the Coast Range of British Columbia and the State of Washington. It has caused serious damage in a number of forest-tree nurseries in the Northern States

and should be carefully considered when a new nursery location is selected. No sweetfern or sweetgale should be tolerated within several hundred yards of a nursery, and no large areas of either should be within 1 mile, if serious loss is to be avoided when weather conditions favor the disease.

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